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Morphological differences between the flowers of *Ramonda serbica*, *R. nathaliae* and their hybrid

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ABSTRACT: Two species of the genus *Ramonda* from the Balkan Peninsula, *R. nathaliae* and *R. serbica* live together forming sympatric populations in only two localities in SE Serbia. In these populations natural hybridization between these two species has been detected employing chromosome number, genome size as well as pollen and seed analysis. It is very difficult to distinguish hybrid individuals from parents directly in the field on the basis of their morphological characters. Investigation of floral traits by traditional morphometry was carried out. The results showed the presence of clear morphological differences between *R. nathaliae* and *R. serbica* as well as pronounced similarity of hybrids with *R. serbica*. Our results showed that the most informative flower characters for distinction of hybrids from *R. serbica* and *R. nathaliae* are the colour of anthers and the angle formed by lines connecting the petal base and points of the maximal petal width. The complex cytogenetic structure of these populations detected in previous studies suggests a complicated and unpredictable character of inheritence in hybrid individuals.

Key words: *Ramonda*, Gesneriaceae, Balkan, sympatry, hybridization, morphometry.

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INTRODUCTION

The family Gesneriaceae comprises c. 3240 plant species mostly distributed in the tropical and subtropical regions of both the Old and New Worlds (Weber 2004). Only a small number of species inhabit temperate regions. Among them, only 5 species of this family are present in Europe: *Ramonda myconi* (L.) Reichenb. - endemic species of the Iberian Peninsula, and *R. nathaliae* Pančić & Petrović, *R. serbica* Pančić, *Haberlea rhodopensis* Friv. and *Jankaea heldreichii* (Boiss.) Boiss. - four endemic species of the Balkan Peninsula. All of them are Tertiary relicts, remnants from the times when the climate was much warmer but also more humid. During climate oscillations in the Ice Age plants were suppressed in shelters in canyons and gorges where they succesfully survived until today.

Balkan species of the genus *Ramonda* are characterized by a disjunct distribution. *Ramonda nathaliae* is restricted to Macedonia, N Greece, slopes of Mt Šara in Kosovo and a few localities in SE Serbia. On the other hand, the largest part of the *R. serbica* range is situated in Albania, though this species is also present in NW Greece, W Macedonia, SW and NE Montenegro, SW, SE and NE Serbia as well as NE Bulgaria. The ranges of two species overlap only in two localities in SE Serbia, Oblik and Radovanski Kamen, establishing sympatric populations.

The first data on the possible co-occurrence of *Ramonda* species in SE Serbia can be found in reports by their earliest investigators, Sava Petrović and Nedeljko Košanin. They cited that both species were present in the gorge of the river Jelašnica and in Mt Suva planina (Petrović 1882; Košanin 1921). However, Košanin (1939) expressed his opinion that the ranges of two species in these areas did not overlap, but only interfaced. In more recent investigations, Stevanović *et al.* (1986) found the zones of their true sympatry in gorges of the rivers Jelašnica and Nišava, within which *R. nathaliae* and *R. serbica* cohabit.

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Table 1. List of studied populations of *Ramonda* species.

Taxa	Locality	Acronym	Latitude, Longitude	Habitat description	Voucher No. (BEOU)
R. nathaliae	Slopes of Mt Suva planina near the village Divljana	RN_DIV	N 43°10'19.3" E 22°18'10"	*Musco-Ramondaetum nathaliae*, north facing rocks, limestone, 346.6 m asl	20638
R. nathaliae	Gorge of r. Nišava (Oblik)	RN_OBL	N 43°19'47.4" E 22°8'44.9"	*Cetereto-Ramondaetum serbicae ramondaetosum nathaliae*, rock crevices, limestone, 418.2 m asl	20637
R. nathaliae	Radovanski kamen above the village Čukljenik	RN_RAK	N 43°17'1.2" E 22°4'23.5"	*Cetereto-Ramondaetum nathaliae*, rock crevices, limestone, 576.7 m asl	20641
R. serbica	Gorge of r. Jelašnica	RS_JEL	N 43°16'56.2" E 22°3'47.1"	*Ceterachi-Ramondaetum serbicae*, north facing rocks, limestone, 290 m asl	10944
R. serbica	Gorge of r. Nišava (Oblik)	RS_OBL	N 43°19'52" E 22°8'43.3"	*Cetereto-Ramondaetum serbicae*, rock crevices, limestone, 279.8 m asl	20634
R. serbica	Radovanski kamen above the village Čukljenik	RS_RAK	N 43°17'4.5" E 22°4'29.2"	*Cetereto-Ramondaetum serbicae*, rock crevices, limestone, 564 m asl	31672
Hybrid	Gorge of r. Nišava (Oblik)	HY_OBL	N 43°19'47.4" E 22°8'44.9"	*Cetereto-Ramondaetum serbicae ramondaetosum nathaliae*, rock crevices, limestone, 418.2 m asl	20636
Hybrid	Radovanski kamen above the village Čukljenik	HY_RAK	N 43°17'5.1" E 22°4'16.6"	*Cetereto-Ramondaetum serbicae ramondaetosum nathaliae*, north facing rocks, limestone, 574.5 m asl	20640

One of those two localities is Radovanski Kamen, situated above the gorge of the river Jelašnica. On that locality, both species live on the northward exposed limestone rocks as well as on rocks within the *Carpinus orientalis* forest. Only one subpopulation of *R. serbica* can be found within the *Fagus moesiaca* forest (Lazarević 2012). *Ramonda nathaliae* seems to be more abundant in this locality where, as the more xerotolerant, this species inhabits the more open microsites than *R. serbica* which is often protected from the direct sunlight by surrounding trees (Stevanović *et al.* 1986).

The other locality, Oblik, is situated on the north exposed side of the gorge of the river Nišava. Here, both species inhabit very steep rocky slopes mostly protected by mixed forest composed of *Acer intermedium*, *Carpinus orientalis*, *Corylus colurna* and *Fagus moeasiaca*. *R. serbica* appeared to be present in somewhat larger numbers than *R. nathaliae* (Stevanović *et al.* 1986).

At nearby locations, populations are composed of either *R. serbica* or *R. nathaliae*. Thus, *R. nathaliae is* present at the Mt Suva planina, whereas *R. serbica inhabits* Mt Svrljiške planine, the gorge of the river Nišava above the monastery Sveta Bogorodica and the gorge of the river Jelašnica (Stevanović *et al.* 1986).

Since the discovery of sympatric populations of *R. nathaliae* and *R. serbica*, the two species were considered to be reproductively isolated (Stevanović *et al.* 1986). However, within recent, extensive cytogenetic investigations hybrids between them were discovered (Siljak-Yakovlev *et al.* 2008). This study showed that a diploid *R. nathaliae* (2n=2x=48) intercrossed with a hexaploid *R. serbica* (2n=6x=144) in two sympatric populations producing mostly tetraploid hybrids with 2n=4x=96 chromosomes. Comparison of pollen and seeds from two parental species and their hybrids clearly showed that pollen grains in hybrids were heterogeneous in size and morphology. Moreover, their seeds were much smaller than in the parental species and were characterized by very low germination ability (Lazarević *et al.* 2013).

In the field it is almost impossible to distinguish hybrids from their parental species, especially from *R. serbica*. This implies the necessity to find morphological characters valuable for more simply distinguishing between them. Therefore, the aim of this study was to determine morphological differentiation of flowers between *R. nathaliae*, *R. serbica* and their hybrids by means of traditional morphometry.

MATERIAL AND METHODS

Plant material. Plant material was sampled from four localities in SE Serbia. Representative samples from one

population of *R. serbica* and one population of *R. nathaliae* were collected in two different localities. In the other two localities, within which *R. nathaliae* and *R. serbica* grow together in sympatry and form hybrid individuals, additional six groups of plants were sampled (two of each of the two species and their hybrid(s)) (Table 1). From each sampling group, 7-20 plant individuals, depending on the population size, were used for morphological analysis of flowers (in total 129 individuals). From each of them, three flowers were analyzed, resulting in 387 analyzed samples. Voucher specimens were deposited in the Herbarium of the Institute of Botany and Botanical Garden, Faculty of Biology, University of Belgrade (BEOU).

Morphometric analysis of flowers was carried out on dissected flowers, well preserved in glycerol: 96% ethanol (50:50, v/v). Measurements of 11 continuous characters were performed with Leica Q Win (Leica Microsystems).

Statistical analysis. Descriptive statistics for each of the characters was performed and the following parameters were obtained: minimum, mean, maximum and standard deviation. Principal component analysis (PCA) was performed on the complete data set (comprising 387 samples and 11 characters) to show the overall morphological variation and relationships between individuals from each population. The differences in PCA scores between populations were tested by a one-way ANOVA (Quinn & Keough 2002). The hypothesis of morphological separation of the four populations was tested by a canonical discriminant analysis (CDA) based on the complete data set of flower characteristics. Multistate descriptors (number of sepals, petals and stamens) were analyzed by Multiple Correspondence Analysis (MCA). Statistical analyses were performed in Statistica 5.1 (StatSoft 1996).

RESULTS

Ramonda serbica and *R. nathaliae* were morphologically clearly distinguished by specific morphological characteristics of their flowers. Flowers of *R. serbica* are cup-shaped; their corolla is formed mostly by five, sometimes by three to six petals with flat margins that do not overlap. On the other hand, flowers of *R. nathaliae* are flat with mostly four, and sometimes with three, five or six petals with undulated margins that overlap. Flowers of their hybrid individuals largely resembled those of *R. serbica* (Figure 1).

Basic statistics of the 11 characteristics revealed only small differences in sepal traits between the two parental species and their hybrids. Dissimilarities among features of petals and stamens were more pronounced (Table 2).

Major differences in morphological characters of flowers between investigated populations were revealed by Principal Component Analysis. PCA showed that the first three principal components, with eigenvalues greater than 1.00, explained most of the structural variability of the populations (80.25%) (Table 3). Most of the variation, 36.46%, was explained by the first principal component (PC1), 33.06% by the second (PC2), and 10.73% by the third (PC3). PC1 mostly described differences in the angle formed by lines connecting the petal base and the points of the maximal petal width (Angle), length from base to the maximal width of the petal (Co_Lm), total length of the petal (Co_Lt) and length of anthers (An_L). Characters contributing to differentiation along PC2 were maximal width of the petal (Co_Wm) and perimeter of the petal (Co_P) (Table 3).

According to the results of PCA, the four populations formed three distinct groups (Figure 2A). The first

Fig. 1. Flowers of *R. nathaliae* (A), hybrids between *R. nathaliae* and *R. serbica* (B) and *R. serbica* (C).

Table 2. Basic statistics of the populations of *R. nathaliae*, *R. serbica* and their hybrid (N-number of plant samples, min-minimum, max-maximum, std-standard deviation). All data in mm, except the angle formed by lines connecting petal base and the point of the maximal petal width (°).

	N	min	mean	max	std	N	min	mean	max	std	N	min	mean	max	std
Character/taxa	*R. nathaliae*					*R. serbica*					Hybrids				
Sepal															
Total length - Ca_l	180	0.20	0.32	0.49	0.05	102	0.21	0.39	0.54	0.07	105	0.27	0.45	0.63	0.06
Base width - Ca_Wb	180	0.14	0.23	0.37	0.04	102	0.12	0.23	0.40	0.04	105	0.14	0.24	0.34	0.04
Width in the upper quarter - Ca_Wq	180	0.06	0.13	0.37	0.04	102	0.05	0.12	0.24	0.03	105	0.05	0.14	0.29	0.04
Petal															
Perimeter - Co_P	180	2.61	4.91	6.82	0.68	102	2.90	4.03	5.53	0.51	105	3.59	5.00	6.13	0.66
Maximal width - Co_Wm	180	0.89	1.44	1.86	0.18	102	1.17	1.54	1.91	0.18	105	1.29	1.75	2.21	0.21
Total length - Co_Lt	180	0.81	1.64	2.36	0.25	102	0.58	1.00	1.64	0.17	105	0.86	1.44	1.90	0.24
Length from base to the maximal width of the petal - Co_Lm	180	0.41	0.61	0.88	0.09	102	0.73	1.03	1.36	0.15	105	0.81	1.13	1.56	0.16
Angle formed by lines connecting petal base and the point of the maximal petal width (°)	180	89.95	127.16	178.33	14.11	102	40.92	58.46	84.50	8.09	105	47.65	73.74	122.76	13.27
Stamen															
Anther length - An_L	180	0.19	0.25	0.30	0.02	102	0.13	0.20	0.26	0.02	105	0.19	0.24	0.28	0.02
Filament length - An2_L	180	0.24	0.35	0.43	0.04	102	0.17	0.29	0.37	0.04	105	0.27	0.35	0.43	0.03
Length of filament base - An3_L	180	0.10	0.21	0.44	0.05	102	0.23	0.32	0.41	0.04	105	0.22	0.34	0.48	0.06

Table 3. PCA-factor loadings for the first, second and third principal component, eigenvalue and % of total variance. Components with loadings larger than 0.7 are marked in bold (for the explanation of character acronyms see Table 2).

	Ca_l	Ca_Wb	Ca_Wq	Co_P	Co_Wm	Co_Lt	Co_Lm	Angle (°)	An_L	An2_L	An3_L	Eigenvalue	% total variance
PC1	0.49	-0.11	-0.19	-0.47	0.27	**-0.77**	**0.78**	**-0.95**	**-0.71**	-0.63	0.65	4.01	36.46
PC2	-0.61	-0.55	-0.52	**-0.79**	**-0.89**	-0.53	-0.57	0.08	-0.37	-0.39	-0.61	3.64	33.06
PC3	0.24	-0.67	-0.69	0.15	0.16	0.1	0.1	0.02	0.19	0.29	0.06	1.18	10.73

principal component separated the populations into two groups. The first group comprised all individuals of *R. nathaliae*, whereas the other group included individuals of *R. serbica* and most of the hybrids. This separation was based mainly on differences in petal dimensions. Namely, in contrast to flowers of *R. serbica* and hybrid individuals, the flowers of *R. nathaliae* have longer petals, wider at the base, with obtuse angle formed by lines connecting the petal base and the point of maximal width, but they also have longer stamens. ANOVA confirmed that the PC1 scores were significantly different among populations ($F_{7,379}$=381.19, P<0.001). The second principal component separated hybrid individuals from both *R. serbica* and *R. nathaliae* because hybrid flowers had wider petals with a larger perimeter. As in the case of PC1, PC2 scores were significantly different among populations ($F_{7,379}$=53.68, P<0.001). Therefore, PCA indicated that the populations of *R. nathaliae* and *R. serbica* were completely separated in the space defined by the first two principal components, whereas hybrid individuals were well separated from *R. nathaliae*, and partially overlap with *R. serbica*.

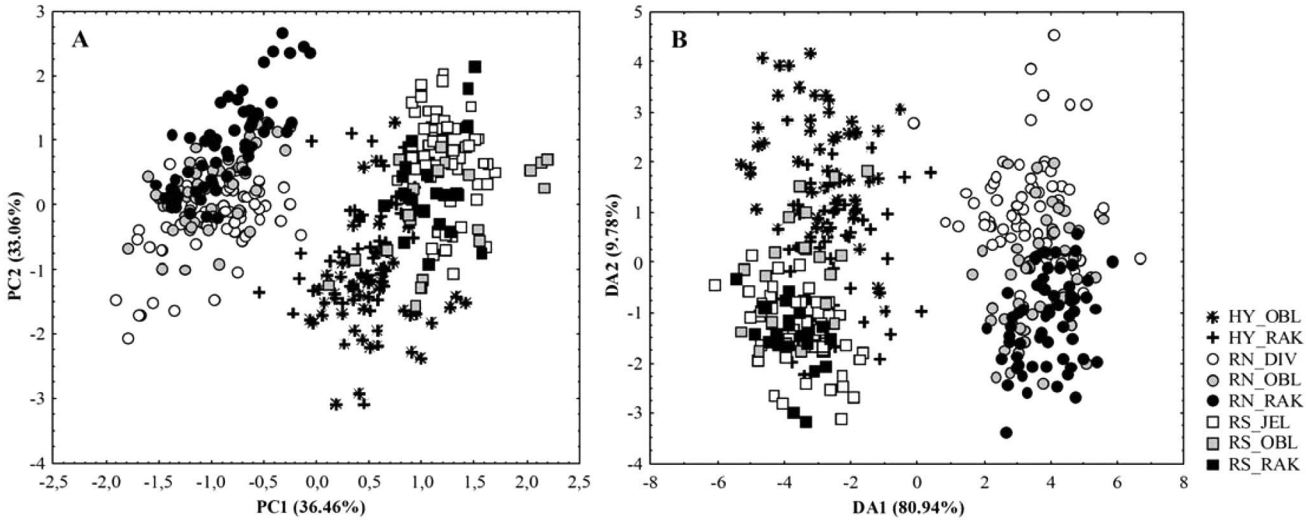

Fig. 2. Principal Component Analysis (PCA) (A) and Canonical Discriminant Analysis (CDA) (B) plotted along the first two axes.

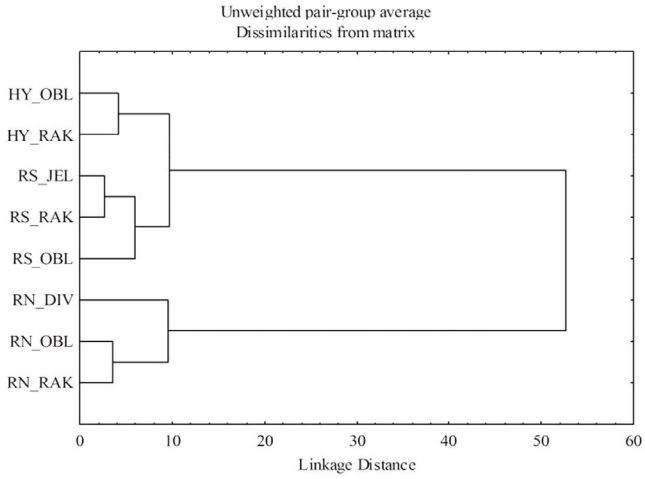

Fig. 3. Cluster analysis (UPGMA) for the populations of *R. nathaliae*, *R. serbica* and their hybrid based on Mahalanobis distances.

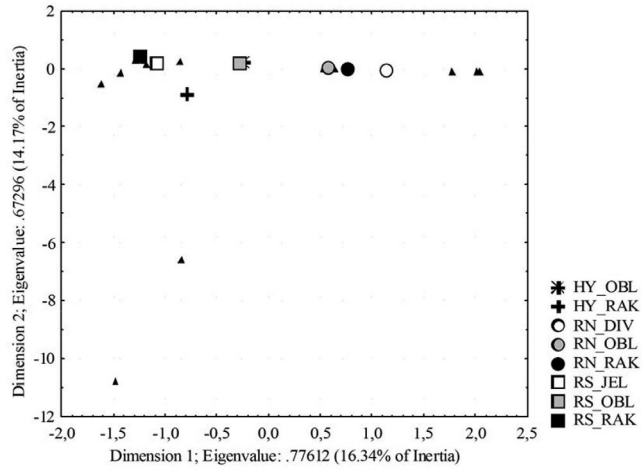

Fig. 4. Multiple Correspondence Analysis of the distribution of populations of *R. nathaliae*, *R. serbica* and their hybrid in relation to the number of sepals, petals and stamens. Triangles represent multistate descriptors.

Canonical discriminant analysis (CDA) showed very strong morphological differentiation of the populations along the first two discriminant axes (DA). On the first DA that explained 80.94% of the variation, populations of *R. nathaliae* were completely separated from the populations of *R. serbica* and hybrid individuals (**Figure 2B**). Within each of these two groups some populations showed a tendency of differentiation along the second DA that explained 9.78% of the overall variation. Thus, *R. nathaliae* from Divljana (RN_DIV) was slightly separated from the other two populations of *R. nathaliae*, as well as from hybrid individuals from Oblik (HY_OBL) due to the somewhat larger petals. Classificatory discriminant analysis showed that 78.3% of the individuals were assigned to the correct population.

Consequently, cluster analysis showed differentiation of populations into two main groups: the first one composed of populations of *R. nathaliae*, whereas the second one comprised two subgroups, one made of populations of *R. serbica* and the other composed of hybrid individuals (**Figure 3**). Clear morphological separation between the populations was also described by overall Mahalanobis distances.

Multiple Correspondence Analysis for multistate descriptors (number of sepals, petals and stamens) confirmed the separation of the four populations (**Figure 4**). The first dimension of MCA separated *R. nathaliae* that was associated with 4 (or 3) sepals, petals and stamens, from *R. serbica* and hybrids, associated with 5, 6 or 7 sepals,

petals and stamens. Additionally, the second dimension separated the hybrids from Radovanski kamen (HY_RAK), due to the presence of individuals with 7 sepals and stamens which were recoded only in this population.

DISCUSSION

Hybridization and polyploidy are some of the most important mechanisms in plant evolution and speciation (Rieseberg & Ellstrand 1993; Rieseberg & Carney 1998; Marhold *et al.* 2002; Ainouche *et al.* 2003; Lihová *et al.* 2007) that have also significantly contributed to the speciation within the palaeotropical Gesneriaceae (Weber 2004). *Ramonda* is one of the genera of this family where polyploidy has played a significant role. Cytogenetic investigations have confirmed the diploid chromosome number in *R. nathaliae* but have also surprisingly revealed that *R. serbica* is a hexaploid, and that there are mostly tetraploid hybrid individuals present within the sympatric populations (Siljak-Yakovlev *et al.* 2008).

Analysis of flower morphological variability using tradional morphometry indicates strong, significant differentiation among *R. nathaliae* and *R. serbica*. Flowers of *R. nathaliae* are (3-) 4-merous, rotate, with overlapping petals and undulate margins. In *R. serbica* they are mostly 5-merous, sometimes 4- and 6-merous and cup shaped, with petals that do not overlap, characterized by flat margins. Petal colour is violet, but is darker in *R. nathaliae* in comparison with *R. serbica*, while anthers are usually yellow in the first and blue-violet in the second species. Flowers of the two species are also clearly different in petal length, the angle formed by lines connecting the petal base and points of maximal petal width, as well as in the anther and filament length; all these parameters being larger in *R. nathaliae*.

Generally, hybrids have a mixture of parental and intermediate flower characters, but are somewhat more similar to *R. serbica*. Thus, their usually cup-shaped flowers are mostly (4-) 5- (6-) merous, but can even be 7-merous. Petals are not overlapping. Anthers are yellow, often with just a hint of blue. Hybrids are similar to *R. nathaliae* concerning petal perimeter, anther and filament length. They are closer to *R. serbica* considering length from the base to maximal width of the petal and length of filament base. Their petal total length and angle formed by lines connecting petal base and the points of maximal petal width are intemediate between the two parental species. However, sepal length and petal maximal width in hybrid individuals exceed these in both parents.

This greater similarity of tetraploid hybrids (2C~5pg) to *R. serbica* was expected because the genome of a hybrid between a hexaploid and a diploid contains three parts of one species (*R. serbica*) and one part of the other species (*R. nathaliae*). However, cytogenetic investigations of sympatric populations have also revealed possible backcrosses of the tetraploid hybrid with *R. serbica* (2C~6 pg) and hybrids with doubled ploidy level (8×) and genome size (2C~9.5 pg) (Siljak-Yakovlev *et al.* 2008). This fact makes character expression in hybrids in these sympatric populations more intricate and unpredictable.

Hybrids between *R. nathaliae* and *R. serbica* that have been detected so far only in two sympatric populations in SE Serbia have not yet spread beyond this range. Most probably the main reason lies in the fact that seed germination capacity in hybrid individuals is extremely low, disabling their expansion by seed dispersal. They multiply mostly by vegetative reproduction (Lazarević *et al.* 2013).

CONCLUSION

Analysis of flower morphology in *R. nathaliae*, *R. serbica* and their hybrids has shown that the most informative flower characters for hybrid distinction seem to be anther colour and angle formed by lines connecting the petal base and the points of maximal petal width according to statystical analyses. It is also clear that morphological characters alone are of limited significance when identifying natural hybrids and that other, primarily cytogenetic and molecular analyses are the keys for their successful detection (Rieseberg & Ellstrand 1993; Rieseberg & Carney 1998).

Are the hybrids more or less fit than the parental species? They are present in large numbers in a sympatric population which suggests that at least in these two habitats they could be more successful than their parents (Tauleigne-Gomes & Lefèbvre 2005; Arnold 1997). However, it has been stated (Arnold & Hodges 1995; Barton and Hewitt 1989) that hybrids are less fit than parental species and that the hybrid zone is maintained through a balance between selection against hybrids and their unceasing production from gene exchanges between the parents. Is is possible that some genome combination will enable them to spread outside these two hybrid zones (Rieseberg 1997). In any case, this hybridization event can have a role in the evolution of the genus *Ramonda*, implying the need for protection of localities where their sympatric populations are situated.

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REZIME

Morfološke razlike između cvetova vrsta *Ramonda serbica*, *R. nathaliae* i njihovog hibrida

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Dve vrste roda *Ramonda* sa Balkanskog poluostrva, *R. nathaliae* i *R. serbica*, žive zajedno u simpatrijskim populacijama na samo dva lokaliteta u jugoistočnoj Srbiji. Na ovim lokalitetima dolazi do prirodne hibridizacije između ove dve vrste što je otkriveno na osnovu broja hromozoma, veličine genoma, kao i analizom polenovih zrna i semena. Međutim, veoma je teško napraviti razliku između hibrida i roditeljskih jedinki na terenu samo na osnovu posmatranja njihovih morfoloških osobina. Zbog toga je u ovom radu urađena detaljna analiza morfoloških odlika cvetova koristeći tradicionalnu morfometriju. Dobijeni rezultati su pokazali postojanje jasnih razlika u morfološkim odlikama cvetova između *R. nathaliae* i *R. serbica*, kao i izražene sličnosti između hibrida i *R. serbica*. Istraživanjem je ustanovljeno da su karakteri cveta koji imaju najveći značaj za razlikovanje hibrida od roditeljskih taksona boja prašnika i ugao koji je dobijen povezivanjem osnove kruničnog listića sa tačkama koje se nalaze na stranama lista a u nivou njegove najveće širine. Složena citogenetička struktura ispitivanih populacija, zabeležena u ranijim radovima, ukazuje na izrazito kompleksno i nepredvidivo nasleđivanje karaktera kod hibridnih individua.

Ključne reči: *Ramonda*, Gesneriaceae, Balkan, simpatrija, hibridizacija, morfometrija.